

Postcranial Evidence of Cold Adaptation in European Neandertals

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ABSTRACT The low brachial and crural indices of the European Neandertals have long been considered indicative of cold adaptation. Recent work has documented lower limb/trunk ratios and deeper chests (anterior-posterior diameter) in European Neandertals than among their successors. The present study uses variables reflective of limb length, body mass and trunk height, and compares European Neandertals to 15 globally diverse recent human samples (1 “Eskimo,” 3 North African, 4 sub-Saharan African and 7 European). Bivariate plots, as well as principal components analysis plots of log shape-transformed data, indicate that European Neandertals had an overall body shape that falls at the extreme end of modern higher latitude groups’ range of variation. Cluster analysis (minimum spanning tree on a principal coordinates plot) indicates that the Neandertals are closest in body shape to modern “Eskimos,” but even in this dendrogram, they are joined to the “Eskimo” via a long branch. In fact, it appears that European Neandertals were “hyperpolar” in body shape, likely due to two factors: 1) the extremely cold temperatures of glacial Europe and 2) less effective cultural buffering against cold stress. *Am J Phys Anthropol* 104:245–258, 1997.

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Recently, the role of climatic adaptation in human evolution has received much attention, particularly with regard to climatic influence on body shape (Trinkaus, 1981; Jacobs, 1983, 1985a,b, 1993; Anderson, 1989; Franciscus, 1989; Stringer, 1989; Holliday and Trinkaus, 1991; Ruff, 1991, 1993, 1994; Holliday et al., 1993; Holliday, 1995). Yet, for one group of fossil hominids, the European Neandertals, there are long-standing hypotheses regarding the role of climate in shaping their morphology (Coon, 1962; Badoux, 1965). In particular, Coon (1962:522) argued that the European Neandertals, living as they did in glacial Europe, gained via “natural selection, the physical features that gave them an advantage for survival in the cold.”

Many of the presumably cold-adapted Neandertal features are believed to be related

to ecogeographical patterning—in particular, Bergmann’s (1847) and Allen’s (1877) “rules.” These rules state that within a widely dispersed species or subspecies of homeothermic animals, those in colder regions will tend to have greater body mass (Bergmann’s rule) and shorter extremities (Allen’s rule) than do their conspecifics in warmer regions. The theoretical explanation for this empirical pattern is that in order to conserve heat in colder regions, homeothermic animals minimize their surface area/volume ratios (SA/V), since heat

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loss in any animal is directly proportional to its surface area. On the other hand, the loss of excess heat in hot environments may be facilitated by a relatively elevated surface area/volume ratio. Increases in body size (Bergmann's rule) tend to reduce this ratio, since surface area only increases proportionally to the two-thirds power of volumetric increase. Allen's rule alters relative surface area in the following way: since the trunk has a lower SA/V ratio than do the limbs, varying the amount of mass in the trunk vs. the limbs affects the relative surface area of the entire organism. For example, an animal with long limbs will tend to have a greater percentage of its mass in its limbs, and is therefore characterized by higher surface area/mass ratios than a shorter-limbed conspecific. It is important to note that Bergmann's rule only alters the SA/V ratio under conditions where shape is maintained despite an increase in size between morphs (i.e., geometric similarity). As a result, Bergmann's rule may be violated under a compensatory change in shape, such as those brought about by Allen's rule.

While exceptions to ecogeographical rules have been cited (Reinig, 1939; Scholander, 1955; Wilber, 1957; McNab, 1971; Geist, 1987), there are numerous studies of widely dispersed homeothermic species (both mammalian and avian) demonstrating their adherence to these rules (Cowan, 1936; Young and Goldman, 1946; Hamilton, 1961; Murphy, 1985; Klein, 1986; Aldrich and James, 1991; Graves, 1991; Paterson, 1996). Evidence for these rules among recent humans is ubiquitous, as well (Coon et al., 1950; Coon, 1962; Schreider, 1950, 1964, 1975; Newman, 1953, 1960, 1961; Newman and Munro, 1955; Roberts, 1953, 1978; Baker, 1960; Crognier, 1981; Trinkaus, 1981; Ruff, 1991, 1994; Holliday, 1995). Thus, as pointed out by Badoux, "since modern humans obey ecological rules, there is absolutely no reason to presume this would not have been the same for fossil humans" (Badoux, 1965, pp. 77–78; translation mine). In this regard, Neandertals provide the best test case for climatic adaptation in non-modern *Homo*, since their sample size exceeds that of earlier members of our genus.

Over the last two decades, there have been many studies of climatic adaptation in

Neandertals. In 1981, Trinkaus provided evidence for cold adaptation in the postcranial skeletons of Neandertals. First, he showed that European Neandertals were characterized by very high claviculo-humeral indices. Trinkaus argued these indices may indicate either larger chest volume in European Neandertals (Bergmann's rule) or short humeri (Allen's rule). He also noted, however, that the claviculo-humeral index is not correlated with climatic factors among recent humans. He then demonstrated that Neandertals (particularly in Europe) exhibit cold-adapted patterning in brachial and crural indices (a fact noted earlier by Coon, 1962, and Badoux, 1965). Distal limb foreshortening was also evident in scatter plots in which radius length was regressed on humerus length and tibial length was regressed on femur length. The Neandertals fell far below the recent human regression line in both of these relationships, indicating that they possessed abbreviated distal limb segments throughout their size range. Trinkaus then plotted brachial and crural indices against mean annual temperature for his recent human groups, which showed that with a decrease in temperature, there was a concomitant decrease in brachial and crural indices. His regression equations have since been corrected and used to predict the mean annual temperature associated with the Nariokotome *Homo erectus* skeleton (30.8°C and 29.2°C for brachial and crural indices, respectively)—demonstrating its tropical sub-Saharan African affinity (Ruff and Walker, 1993). Applying these equations to a sample of Western European Neandertals (Holliday, 1995), the mean brachial index of 73.2 and the mean crural index of 78.7 predict mean annual temperatures of 2.4°C and -1.7°C, respectively. While there is obviously error inherent in predicting mean annual temperature from morphological variables, the fact that the Neandertal predicted temperatures are so low can almost certainly be taken to reflect cold adaptation.

Holliday and Trinkaus (1991) have more recently shown that European Neandertals are characterized by short proximal and particularly short distal limb segments relative to skeletal trunk height. Importantly, limb/trunk ratios segregated European from West Asian "Neandertals," with the Euro-

TABLE 1. *List of European Neandertal specimens included in the study*

Specimen	Sex	Archeological association	Date
La Chapelle 1 ¹	M	Charentian Mousterian (Quina) ²	47 ± 3/56 ± 4 Kya (EU/LU ESR) ³
La Ferrassie 1 ⁴	M	Charentian Mousterian (Ferrassie) ⁵	ca. 72 Kya (Stratigraphic comparison with Le Moustier) ⁶
La Ferrassie 2 ⁴	F	Charentian Mousterian (Ferrassie) ⁵	ca. 72 Kya (Stratigraphic comparison with Le Moustier) ⁶
Neandertal 1 ⁷	M	None	Early Würm ^{7,8}
Régourdou 1 ^{9,10}	?	Charentian Mousterian (Quina) ¹¹	Early Würm ^{7,8}
Spy 2 ¹²	M	Mousterian ¹³	Early Würm ¹³

¹ Boule (1911–13); ² Vandermeersch (1965); ³ Grün and Stringer (1991); ⁴ Heim (1982); ⁵ Bourgon (1957); ⁶ Mellars (1986); ⁷ Schwalbe (1901); ⁸ Oakley (1964); ⁹ Piveteau (1963–66); ¹⁰ Vandermeersch and Trinkaus (1995); ¹¹ Bonifay and Vandermeersch (1962); ¹² Fraipont and Lohest (1887); ¹³ Zeuner (1940).

pean Neandertals appearing more cold-adapted. This study, however, suffered from a relatively small sample of both recent and fossil humans. The current study is designed to re-examine claims of postcranial cold adaptation in European Neandertals, specifically as reflected in body shape. This study brings into play two important new additions. The first is a larger sample of recent humans to which the Neandertals may be compared, and the second is multivariate analyses of size and shape, which allow us to examine whether differences in body shape are driven by changes in body size.

MATERIALS AND METHODS

Materials

The Western European Neandertals who preserve body proportion information are few ($n = 6$), and are listed in Table 1. All specimens were measured by the author; raw measurements for the specimens are found in Holliday (1995).

Summary statistics for the 15 recent human samples (total $n = 821$) are found in the Appendix. With the exception of the East African sample, provided by C.B. Ruff, the Anglo-Saxon data, from Münter (1936), and some of the San data, taken from Slome (1929), all samples were measured by the author. They represent groups from widely variable ecogeographic zones, spanning tropical to Arctic regions. All groups have been placed into four discrete regional categories (Circumpolar, Europe, North Africa, sub-Saharan Africa) for many of the analyses. Two things are important to note, however. First, the "Circumpolar" group is represented solely by Koniag "Eskimos." This group is found on or near Kodiak Island,

Alaska, and are thus not a high arctic group. Nonetheless, from a global and population historical perspective, they are a high latitude, cold-adapted group, and are the only "Eskimo" group for whom associated skeletons were available for study. Second, the Sudanese sample from Kerma straddles the "boundary" between supra- and sub-Saharan Africa, and could easily be subsumed into either subsample. For more detailed discussion of the recent human samples, see Holliday (1995).

Methods

The measurements used in this analysis are femoral A-P head diameter (FHAP), skeletal trunk height (STH), femoral bicondylar length (FL), humeral maximum length (HL), tibial maximum length (TL) and radius maximum length (RL). All of the measurements reflect either trunk height, body mass, or the lengths of the four major limb segments. These measurements provide an accurate assessment of limb and body proportions as well as overall body size. With the exception of skeletal trunk height, all measurements are standard osteometrics. Skeletal trunk height is defined as the summed dorsal body heights of the thoracic and lumbar vertebrae plus sacral ventral length (Franciscus and Holliday, 1992). None of the European Neandertals preserves all of its components, and therefore skeletal trunk heights were predicted from partial trunk height (i.e., subset of preserved elements) using least-squares regressions based on a complete recent human series ($n = 45$) (Table 2). These predicted trunk heights are accurate, as reflected in the standard error of prediction (Table 2). In no case was a predicted trunk height used if its standard

TABLE 2. Predictive equations for skeletal trunk height on partial trunk height for European Neandertal specimens

Specimen	Vert. (N)	β	Y-intercept	r^2	\hat{Y}	SE \hat{Y}	% of \hat{Y}	95% C.L.
La Chapelle-aux-Saints	9	2.165	50.452	0.936	482.7	9.437	1.96%	463.7–501.7
La Ferrassie 1	7	2.934	61.527	0.903	514.3	11.722	2.28%	490.7–537.9
Régourdou 1	8	2.608	32.748	0.927	498.2	10.113	2.03%	477.8–518.6

error of prediction was greater than 3% of the predicted measurement. Trunk height was also predicted for a subsample of the recent humans ($n = 50$) who did not preserve all its elements, but as with the fossils, none was accepted if it did not meet the above stringent criterion.

Finally, for the East African sample, maximum femoral length was transformed to bicondylar length using a regression formula based on recent Amerindians ($n = 40$). The mean standard error of prediction for bicondylar from maximum length was less than 1% of the predicted measurement, indicating that prediction error is less than standard measurement error.

In order to demonstrate that the features examined show ecogeographical patterning among modern human groups, the correlation between sample means of the skeletal features of the recent human groups and latitude is examined. Latitude is readily available for most groups, since they are comprised of individuals from a single site. However, for five groups (East and West Africans, San, Pygmy and Anglo-Saxons) latitude is an arithmetic average, since these samples are comprised of individuals from multiple sites. This is unlikely to have biased results, since all significant results remain significant when the groups for whom latitude was estimated are removed. The latitudes used in correlation analyses are given in the Appendix.

Bivariate analyses

Statistical analyses of the fossils begin with examination of bivariate plots and associated indices. Simply put, the location of the fossils in bivariate space relative to recent human groups will elucidate two-variable proportional relationships among the samples. Indices provide a second means of assessing simple proportional relationships. These analyses (bivariate plots and

indices) have the advantage of including all of the fossil specimens, and provide a baseline that can then be used to interpret the multivariate analyses.

Multivariate analyses

Multivariate analyses begin with the computation of "log size-and-shape" and "log shape" variables, following Mosimann and colleagues (Mosimann and James, 1979; Darroch and Mosimann, 1985; James and McCulloch, 1990). Log size-and-shape variables are the log-transformed raw measurements. Shape variables are "scale-free" indices produced by computing the ratio of each variable with the geometric mean of all the measurements for that individual. Darroch and Mosimann (1985) have argued that the geometric mean of an individual's measurements is the best measure of that individual's overall size. These ratios are therefore scale-free, since an isometric size component has been removed from each variable. Importantly, this method is not merely the removal of the effects of size on shape per se. In fact, size and shape may be correlated, and this can be tested using shape variables; a significant negative correlation of a shape variable with the geometric mean indicates a subisometric relationship, a significant positive correlation coefficient is indicative of a supraisometric relationship, and a non-significant correlation indicates the shape variable is characterized by an isometric relationship with increasing size.

This method of shape extraction is superior to examination of residuals from an allometric relationship, since shape is intrinsic to the individual, and not a function of the comparative sample. Put simply, it is known that an individual's residual from an allometric relationship based on a sample will change with sample size and/or constituency, while it is obvious that the individual's own shape has remained unchanged. Both

the "log size-and-shape" and "log shape" variables are subjected to principal components analysis (PCA) based on the variance-covariance matrix (VCM). By comparing the eigenvalues from the two matrices, one can determine what percentage of the total variance is explained by a combination of size and shape vs. shape alone. This is important in understanding the amount of shape information present in the variable set. All PCAs were performed using NCSS version 4.21 (Hintze, 1986).

Cluster analysis

The phenetic affinities of the groups are elucidated via a clustering method, as well. Since body shape is the primary variable of interest, the group means for the log shape data will be subjected to principal coordinate analysis (PCO) with minimum spanning tree (Prim, 1957; Howard, 1991). The resulting dendrogram serves as a variable evolutionary rate tree based on a Euclidean distance matrix. The PCO and minimum spanning trees were performed using a PC version of NTSYS (Rohlf, 1990).

RESULTS

Bivariate analyses

Among the 15 recent human groups, both brachial and crural index means exhibit a significant, negative correlation with latitude ($r = -0.75$ and -0.88 , respectively). This result holds even when the sexes are examined separately, or when the small-bodied human groups (Pygmy and San) are removed from the analysis. Thus, among recent humans, increases in latitude, and hence, generally increasingly colder climes, are associated with decreases in brachial and crural indices.

Summary statistics for brachial and crural indices, computed by geographic region, are found in Table 3. Among the recent humans, the Koniag "Eskimo" exhibit lower crural indices than any of the other groups. Their brachial indices are also low, although as a whole, the European sample exhibits a slightly lower mean value. As a result, while the Koniag have a significantly lower crural index than the recent Europeans ($P = 0.0004$), they do not differ significantly from the recent Europeans for the brachial

TABLE 3. Summary statistics for Neandertal and recent human samples—crural and brachial indices

	Crural index	Brachial index
European Neandertals		
\bar{X}	78.7	73.2
SD (n)	1.6 (4)	2.5 (5)
Koniag ("Eskimo")		
\bar{X}	80.5	75.3
SD (n)	2.3 (20)	2.6 (20)
Recent Europeans		
\bar{X}	82.7	75.0
SD (n)	2.4 (436)	2.5 (391)
Recent North Africans		
\bar{X}	85.0	78.6
SD (n)	2.3 (133)	2.4 (136)
Recent sub-Saharanans		
\bar{X}	86.1	79.6
SD (n)	2.2 (66)	2.5 (67)

index ($P = 0.62$). What is of interest in Table 3 is the position of the Neandertals, who have lower brachial and crural indices than any of the recent human samples. Relative to the Koniag "Eskimo," the Neandertals show a tendency toward lower (although not statistically significantly lower) brachial and crural indices ($P = 0.06$ and 0.07 , respectively).

An index of femoral head diameter to femoral length has been used as a measure of relative body linearity by several workers (Ruff, 1987, 1990, 1994; Franciscus, 1989; Jungers, 1991). Since Bergmann's rule predicts that body mass will increase with latitude, while Allen's rule predicts that the extremities will get shorter as latitude increases, we should expect that a skeletal reflection of body size (femoral head), scaled to a measure of body linearity (femoral length), will show ecogeographical patterning in modern humans. When such a FHAP/FL ratio is examined among the 14 recent human samples for which femoral head data are available, there is a significant correlation between this index (14 sample means) and latitude, such that higher latitude groups tend to be characterized by relatively larger femoral heads ($r = 0.69$; $P < 0.0001$). Importantly, this result holds both when the sexes are analyzed separately, and when the small-bodied Pygmies and San are removed from the analysis.

Figure 1 is a scatter plot of femoral head diameter (FHAP) on femoral length (FL) for the recent humans ($n = 471$) and the European Neandertals ($n = 5$). Note that while

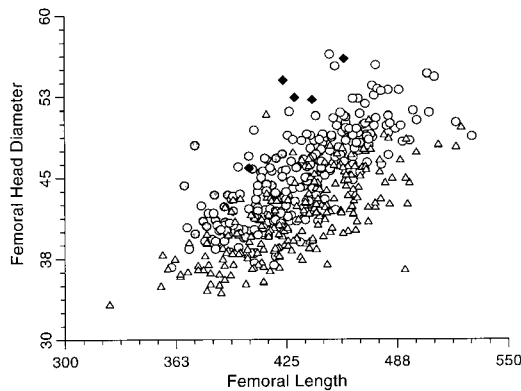


Fig. 1. Scatter plot of femoral head diameter on femoral length. Open circles, Recent Europeans; triangles, Recent Africans; gray circles, Koniag "Eskimo"; black diamonds, Neandertals.

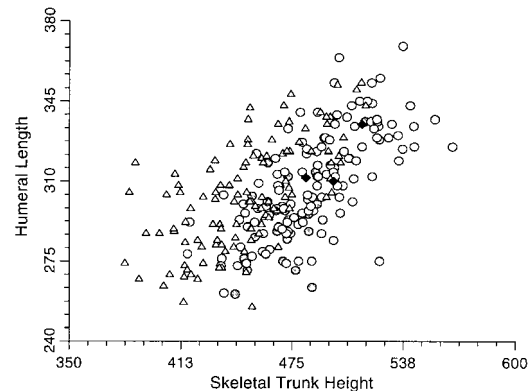


Fig. 2. Scatter plot of humeral length on skeletal trunk height. Open circles, Recent Europeans; triangles, Recent Africans; gray circles, Koniag "Eskimo"; black diamonds, Neandertals.

there is considerable overlap among the recent broad geographic samples, there is a tendency for the Europeans and "Eskimos" to have larger femoral heads for any given femoral length than the Africans. The one African individual who greatly deviates from this tendency is a member of a Nubian sample thought by its excavators to represent then-recent immigrants to the region (Elliot Smith and Wood Jones, 1910). Thus non-African nativity could explain his unusual position in bivariate space.

All but two of the Koniag "Eskimos" lie within the European scatter, although they tend to fall toward the high end of the European range. Note, too, the extreme position of the five Neandertals (Régourdou 1 is absent, since it lacks a preserved femur) relative to the recent human groups, including the Koniag. In fact, if for this relationship 95% confidence limits are put about either the 20 Koniag or 233 European individuals, only one of the five Neandertals (La Ferrassie 2) would fall within those limits. Therefore, in this regard, the relative size of the Neandertal femoral head diameters appears "hyperpolar."

The length of the limb segments relative to the trunk provides yet another assessment of body proportions. Figure 2 is a scatter plot of humeral length on skeletal trunk height for the recent humans ($n = 258$) and Neandertals ($n = 3$). Note that while there is much overlap among the recent

geographical samples, there is nonetheless a clear tendency for the Africans to have longer humeri relative to their trunk height than do the Europeans or the Koniags. The Neandertals possess proximal limb segments which are not unlike those of recent Europeans; the three Neandertals who preserve sufficient vertebral elements to reconstruct skeletal trunk height (La Chapelle-aux-Saints 1, La Ferrassie 1 and Régourdou 1) all fall well within the scatter of recent Europeans for this relationship.

There is clearer evidence of ecogeographical patterning among recent humans for distal limb segments on trunk height, as seen in the plot of tibial length on skeletal trunk height (Fig. 3). Here among the 256 recent humans sampled, there is much less overlap between the low and high latitude groups, such that the Africans and Europeans are more separated in bivariate space. While not revealed in the plot, the Africans closest in shape to the Europeans are North Africans. Also, while there is considerable overlap in bivariate space between the Koniag and the Europeans, the former are somewhat differentiated from the latter in that they tend to have shorter tibiae for any given trunk height than do the other samples. The Neandertals (represented solely by La Chapelle-aux-Saints 1 and La Ferrassie 1), however, while possessing somewhat shorter tibiae for any given trunk height than do Europeans on average, none-

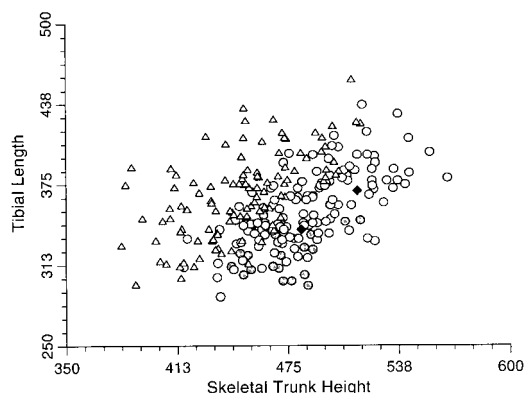


Fig. 3. Scatter plot of tibial length on skeletal trunk height. Open circles, Recent Europeans; triangles, Recent Africans; gray circles, Koniag "Eskimo"; black diamonds, Neandertals.

theless fall well within the recent European scatter for this relationship, as well.

These trends are corroborated by limb/trunk ratios (Table 4). The mean of each of these ratios for the 13 recent human samples who preserve trunk data is significantly ($P < 0.05$) correlated with latitude, whether sexes are combined or analyzed separately, and the fit improves if the small-bodied Pygmies are excluded from the analysis. Table 4 reveals this ecogeographical pattern, as a latitudinal decrease (from sub-Saharan to North Africa, and then from Europe to the Koniag) is evident in all four relative limb segment length indices. Note that the Neandertals have mean values most similar to either the recent Europeans (for proximal limb segments), or to the shortest-limbed Koniags (e.g., as for the radius).

Principal components analysis

The eigenvalues and eigenvector coefficients for the PCA of the log size-and-shape and log shape variables (full variable set: all six measurements) are presented in Table 5. PC1 of the log size-and-shape variables accounts for 75.2% of the variance, and is best interpreted as a size component, since all its eigenvector coefficients are positive and since the scores along this axis are highly correlated with log size ($r^2 = 0.999$, $P < 0.0001$). PC2 (which accounts for 15.6% of the variance) contrasts femoral head diameter and skeletal trunk height with distal limb seg-

ment lengths. The scores along this axis are not significantly correlated with log size ($r^2 = 0.001$, $P = 0.6813$).

Figure 4 is a plot of PC2 on PC1 for the log size-and-shape data. The plot includes individual PC scores for the recent human groups and for the two Neandertal specimens who preserve all six measurements (La Chapelle-aux-Saints 1 and La Ferrassie 1). Note that for PC1 (a size component) the Neandertals have relatively high scores, although well within the recent human range. In fact, there is much overlap among the PC1 scores (i.e., log size) among the recent human groups. This is despite the fact that the Europeans have larger body *mass* variables (e.g., femoral heads) than the Africans. Thus log size in this case is not equivalent to body mass, and the similarity in PC1 scores among these groups is due to the fact that the long limbs of the Africans and the large femoral heads of the Europeans tend to balance each other out in the computation of "log size." Note that the Koniag, who (unlike most of the groups analyzed) are characterized by both smaller femoral heads *and* shorter limbs, have accordingly small PC1 scores.

PC2 separates the long-limbed, short-trunked, and small femoral head-bearing Africans above from the remainder of the groups below, who have larger femoral heads, longer trunks and shorter limbs. As such, PC2 could be considered an ecogeographical, or cold/heat adaptation, component. On average, the more cold-adapted Koniags tend to have smaller PC2 scores than do the Europeans. Note, too, that the Neandertals tend to be more extreme than the Koniags for this component; only one of the 19 Koniags sampled has a lower PC2 score than the two Neandertals, and none of the 109 Europeans (not to mention Africans) sampled has a PC2 score as low as that of the Neandertals.

The reduction in total variance from the log size-and-shape to the log shape analysis indicates that 25.9% of the variance is due to shape. As is often the case with the Darroch and Mosimann method, PC1 of the log shape data is similar to PC2 of the log size-and-shape data. This component explains 61% of the variance and contrasts femoral head diameter and trunk height with distal limb segment lengths. The scores along this axis

TABLE 4. Summary statistics for Neandertal and recent human samples—limb segment/trunk height ratios

	FL/STH	TL/STH	HL/STH	RL/STH
European Neandertals				
\bar{X}	89.1	71.2	64.0	47.0
SD (n)	0.0 (2)	1.0 (2)	1.5 (3)	0.2 (3)
Koniag ("Eskimo")				
\bar{X}	84.3	67.9	62.0	46.6
SD (n)	3.9 (20)	3.5 (21)	3.5 (21)	2.7 (20)
Recent Europeans				
\bar{X}	88.6	73.6	63.6	47.9
SD (n)	2.4 (123)	4.3 (124)	3.4 (124)	2.8 (123)
Recent North Africans				
\bar{X}	94.2	79.8	66.0	51.9
SD (n)	5.5 (63)	4.9 (60)	3.8 (62)	3.4 (62)
Recent sub-Saharan				
\bar{X}	99.3	85.5	70.2	55.8
SD (n)	6.7 (43)	5.9 (43)	4.0 (43)	3.7 (43)

TABLE 5. Principal components of log size-and-shape and log shape variables—full variable set (six variables): Neandertals and recent humans

	Eigenvector coefficient			
	Log size-and-shape		Log shape	
	I	II	I	II
FHAP	0.446	-0.646	0.595	-0.683
FL	0.414	0.196	-0.217	0.011
TL	0.439	0.406	-0.431	-0.022
HL	0.401	0.087	-0.106	0.049
RL	0.435	0.334	-0.360	-0.080
STH	0.296	-0.510	0.520	0.724
Eigenvalue	0.0322	0.0067	0.0068	0.0026
% total variance	75.17	15.64	61.12	23.09

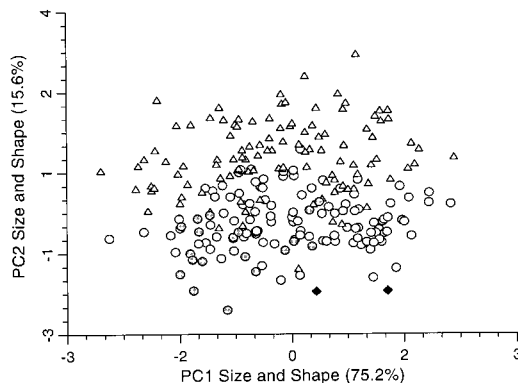


Fig. 4. Principal component 2 on principal component 1 (log size-and-shape). Open circles, Recent Europeans; triangles, Recent Africans; gray circles, Koniag "Eskimo"; black diamonds, Neandertals.

are not significantly correlated with log size ($r^2 = 0.0107$, $P = 0.0893$). PC2 of log shape explains 23% of the variance and contrasts femoral head diameter with skeletal trunk height. The scores along this axis are signifi-

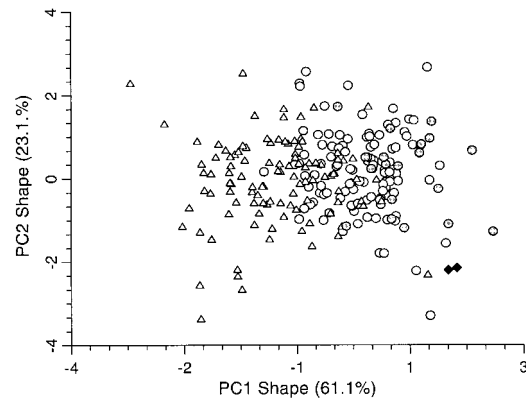


Fig. 5. Principal component 2 on principal component 1 (log shape). Open circles, Recent Europeans; triangles, Recent Africans; gray circles, Koniag "Eskimo"; black diamonds, Neandertals.

cantly, although not highly, correlated with log size ($r^2 = 0.13$, $P < 0.0001$).

Figure 5 is a plot of PC2 of shape on PC1 of shape. Note the separation of the Africans from the non-Africans (albeit with overlap) along the first principal axis. Recall that this component contrasts those groups and individuals on the left who have small femoral heads, short trunks and long distal limb segments (heat-adapted) with those on the right, who possess longer trunks, large femoral heads and short distal limbs (cold-adapted). The Neandertals have among the largest scores for this component; of the 211 modern humans sampled, only two Koniags meet or exceed the smaller of the Neandertals' (La Ferrassie 1's) value, and as a group, it is the Koniags who most closely approximate the Neandertal condition. Lastly, since

TABLE 6. Principal components of log size-and-shape and log shape variables—reduced variable set (four variables): Neandertals and recent humans

	Eigenvector coefficient			
	Log size-and-shape		Log shape	
	I	II	I	II
FHAP	0.545	−0.824	0.849	0.164
FL	0.463	0.250	−0.235	−0.485
HL	0.480	0.195	−0.176	−0.426
RL	0.508	0.470	−0.439	0.746
Eigenvalue	0.0243	0.0043	0.0043	0.0008
% total variance	81.53	14.43	77.72	13.85

PC2 is correlated with log size, it tends to separate (albeit with significant overlap) males and females. As the two Neandertals are male, on the plot they appear somewhat extreme for this component.

In order to include more Neandertals, a subset of the above variables was used, including FHAP, FL, HL and RL. The variables in this reduced variable set were retained because of the original measurements, these four were preserved in more Neandertal skeletons. Table 6 reports the eigenvalues and eigenvectors for the PCA of the four variables (first two components only). PC1 of log size-and-shape explains 81.5% of the variance. As before, it is best interpreted as a size component, since all its eigenvector coefficients are positive, and since scores along this axis are highly correlated with log size ($r^2 = 0.999$, $P < 0.0001$). PC2 explains 14.4% of the variance. Scores along this axis are not significantly correlated with log size ($r^2 = 0.0004$, $P = 0.6631$), and the component contrasts femoral head diameter with radius length.

The reduction in variance from the log-size-and-shape to the log shape analysis indicates that 18.7% of the total variance is due to shape. Thus, we have lost some shape information by dropping two variables from the previous analysis (TL and STH). The first shape component accounts for 77.7% of the shape variance, and contrasts femoral head diameter with distal limb segment (i.e., radius) length. The factor scores along this axis are significantly, but not highly, correlated with log size ($r^2 = 0.008$, $P = 0.0409$). PC2 of the log shape data explains 13.9% of the variance. It contrasts femoral and humeral length with radius

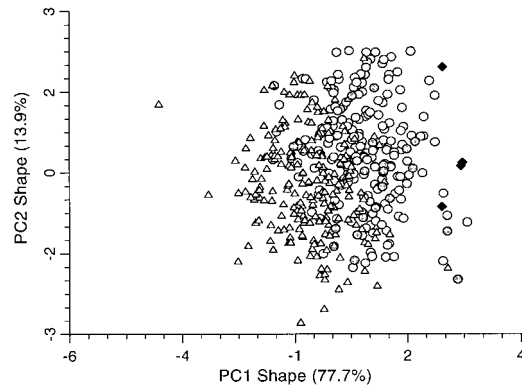


Fig. 6. Principal component 2 on principal component 1 (log shape—reduced variable set). Open circles, Recent Europeans; triangles, Recent Africans; gray circles, Koniag "Eskimo"; black diamonds, Neandertals.

length. The scores along this axis are also significantly, but not highly, correlated with log size ($r^2 = 0.047$, $P < 0.0001$).

Figure 6 is a plot of PC2 of shape on PC1 of shape. Note that there is much more overlap among the recent human groups along PC1 than there was with the analysis of the full variable set. As with the previous analysis, the Neandertals, with their large femoral heads and short radii, have among the highest PC1 (or cold-adapted), scores. In fact, of the modern sample, only four of 217 Europeans (1.8%), one of 130 North Africans (0.8%), two of 19 Koniags (10.5%) and none of the sub-Saharan Africans have higher PC1 scores than the Neandertal individual with the lowest score (Neandertal 1).

Among the recent humans, the Africans, with their small femoral heads and long radii, tend to fall toward the heat-adapted, or left side of the plot, while the Koniag and Europeans, although not as extreme on average as the Neandertals, tend to fall more toward the cold-adapted, or right side, of the plot. PC2 segregates neither the groups nor the sexes.

Cluster analysis

A Euclidean distance matrix between the means of the log shape data (full variable set) was subjected to principal coordinate analysis, and a minimum spanning tree was fit to the coordinate scores. The plot of principal coordinate 2 on principal coordi-

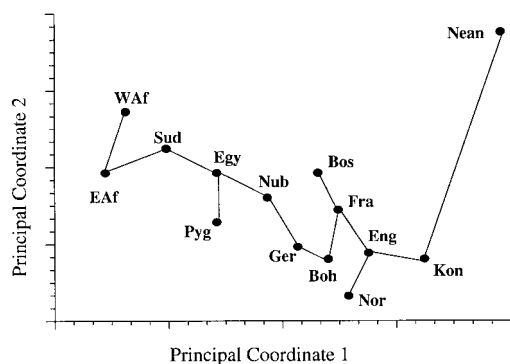


Fig. 7. Principal coordinate 2 on principal coordinate 1 with minimum spanning tree, full variable set, shape data.

nate 1 for the log shape data and its associated minimum spanning tree is found in Figure 7. The first principal coordinate explains 81.1% of the trace, and, as in the principal components plots, contrasts groups based on femoral head size and distal limb length. The second principal coordinate explains 15.2% of the trace, and separates the Neandertals from the remaining groups, most likely due to the male bias of the fossil sample.

The minimum spanning tree provides several interesting links between groups. First, the Neandertals are most closely aligned (albeit at some distance) with the Koniag. The Koniags in turn are linked to a cluster of Europeans, but are closest to the English and Norse. In the middle of the European portion of the tree are clustered the French, Bosnians, Bohemians and Germans. The most linear of the European groups (the Germans) are then linked to the somewhat (curiously?) cold-adapted Nubians. Recall that this group may represent recent émigrés. At the other end of the tree, the East/West Africans and Sudanese are most closely linked to each other, and are subsequently joined to a North African/Pygmy cluster via the Egyptians. This North African/Pygmy cluster is then ultimately linked to the Europeans, as discussed above. One might find it odd that the Pygmies cluster with the North Africans. This is due to allometric effects associated with their small size. In particular, HL-shape exhibits negative allometry,

while FHAP-shape exhibits positive allometry (Holliday, 1995). Therefore, as a result of their small size, the Pygmies are characterized by small femoral heads and long humeri—features aligning them more closely with the North Africans than with sub-Saharan Africans.

DISCUSSION

There are many patterns which have been elucidated by the various analyses. First, in a bivariate sense, the European Neandertals are characterized by the following postcranial features: 1) they possess on average the largest femoral heads relative to femoral length of any of the human groups studied, and 2) they possess short distal limb segments relative to trunk height (or relative to proximal limb segment length). The combination of these features in multivariate space even further segregates the Neandertals from the recent human samples. For example, according to PCA, they tend to fall at the extreme end of modern high latitude groups' ranges. Likewise, the minimum spanning tree fit to the PCO plot clusters them most closely with the Koniag "Eskimo," albeit at a considerable distance.

In fact, the phenetic relationship between the Neandertals and the Koniag "Eskimo," a recent cold-adapted group, is of great interest. The Koniag more closely approach the Neandertals in overall body shape than do any of the European groups here analyzed. Yet, importantly, in cluster analyses (including some methods not reported here), the Neandertals are joined to the Koniag via long branches, so extreme is their cold-adapted morphology. Also, according to the PCA plots, few Koniag (perhaps 10%) have as extreme a cold-adapted morphology as the Neandertals. In short, the Neandertals are characterized by a "hyperpolar" morphology, with a long trunk, large femoral heads and short limbs (particularly distal limb segments). Recent work by Churchill (1994a, 1994b) has suggested they may also have had antero-posteriorly deep chests, and it appears, too, that they had wide bodies, as reflected in bi-iliac breadth (Ruff et al., 1993; Ruff, 1994; Holliday, 1995). This last variable, however, can only be approximated for

one European Neandertal (La Chapelle-aux-Saints 1).

Importantly, too, the Darroch and Mosi-mann technique reveals that there is considerable shape variation in the variables analyzed. For both variable sets, the percentage of overall variability explained by shape was around 20–25%. This is a considerable amount of shape information considering that the study is restricted to large postcranial measurements within a single genus. Yet Neandertal body shape, as important as it is, is not the sole feature reflective of cold adaptation. Given Bergmann's rule, body size can also be an important aspect of cold adaptation. In this regard, the European Neandertals appear to have been characterized by high body mass, perhaps 30% greater than high latitude populations today (Ruff et al., 1997). With regard to the data analyzed here, they possess femoral heads within the size range of the recent Europeans, but outside of the range of the other regional samples. Likewise, their geometric means of the measurements used in multivariate analyses (considered by many to be the best reflection of overall size) are larger than all of the recent human sample means.

One consideration, given the high body mass of the Neandertals, is that size is driving their body shape, i.e., their cold-adapted shape is an allometric consequence of their large size. Yet there are several lines of evidence which argue against this hypothesis. First, of the recent human samples, it is the group with one of the smallest mean body sizes (the Koniags) who most closely resemble the Neandertals in body shape. Secondly, the scores along the principal axes which separate the Neandertals from the other groups are either not significantly correlated with log size, or, at most, exhibit a significant, but very weak, correlation. Finally, of the individual shape traits which separate the Neandertals from the remaining groups, only one (FHAP) is correlated with log size such that the Neandertal shape follows allometric expectation. The other variables which distinguish the Neandertals (i.e., distal limb segment lengths) are not significantly associated with log size (Holliday, 1995). Thus, allometric effects alone cannot explain Neandertal body shape.

Finally, we must consider the possible reasons why the Neandertals appear so cold-adapted in the postcranial skeleton. The extremely cold-adapted morphology of the European Neandertals is likely due to two non-mutually exclusive reasons. The first is that the extremely low temperatures in glacial Europe resulted in a large selective coefficient for body shape. Of the Neandertals used here, all are presumably from glacial time periods (Table 1). In this regard, an associated skeleton of an interglacial European Neandertal would be of great interest. Would it exhibit a different body shape?

The second explanation for Neandertal cold-adapted proportions is that cultural buffering in the Neandertals was less effective in reducing selection pressure on body form. With regard to cultural buffering from cold, the Mousterian (with which the majority of Neandertals are associated) is characterized by unsophisticated cultural buffering. In contrast, there are many documented improvements in cultural buffering associated with the Upper Paleolithic (which is generally, but not exclusively, associated with modern humans). More specifically, the Upper Paleolithic is characterized by significant improvements in clothing, pyrotechnology and shelter (Perlès, 1977; Straus et al., 1980; Binford, 1982; articles in Olive and Taborin, 1989; Rigaud, 1989).

For example, it is in the Upper Paleolithic that we find the first solid, consistent evidence for the systematic construction of complex hearths. Regarding clothing, Aurignacian "punches" or "awls" (tool types not found in Mousterian contexts) may indicate humans were binding clothing together with strips of hide. The even later (Solutrean) appearance of the eyed needle (Stordeur-Yedid, 1979) almost certainly represents an innovation in clothing technology. Evidence for shelters in Mousterian (or earlier) contexts is minimal, at best. In contrast, the evidence for structures in the Upper Paleolithic is ubiquitous. All of these thermal improvements may well have reduced selective pressure on body form, explaining why none of the recent human samples (including the Koniag) is as biologically cold-adapted as are the European Neandertals.

One cautionary statement is warranted, however. As mentioned before, the Koniag are not a high arctic group, and as such, may not approximate the current human extreme in cold-adapted morphology. Therefore a comparison of the Neandertals to truly high arctic groups, such as the those living in Greenland, the north shore of Alaska or the Canadian archipelago could prove enlightening. Perhaps these recent groups would more closely approximate the Neandertal condition. At least one reason to suspect they would not, however, is that their system of cultural buffering is far more complex than that of the Neandertals.

CONCLUSIONS

European Neandertals are characterized by an overall postcranial morphology that can be described as "hyperpolar"; their limb and body proportions are extremely cold-adapted, and seem to follow expectations derived from Bergmann's and Allen's rules. The explanation for European Neandertal body shape is multifaceted. Importantly, allometric effects alone do not appear to account for the suite of cold-adapted Neandertal features. Rather, intense selection pressure, due to the cold of glacial Europe and/or less effective buffering against that cold, are probably largely responsible for Neandertal body shape.

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Appendix. Summary statistics (means, standard deviations and sample sizes) for the recent human comparative samples

		FHAP		FL		TL		HL		RL		STH	
		M	F	M	F	M	F	M	F	M	F	M	F
Circumpolar													
Koniag	\bar{X}	45.0	41.6	410.7	385.8	332.0	309.6	308.0	277.4	230.5	210.6	479.9	466.4
L ¹ = 58.0	SD	2.3	2.1	23.7	11.3	14.9	9.0	14.2	11.5	10.5	7.4	19.1	16.6
	n	9	10	10	10	11	10	11	10	10	10	11	10
Europe													
Bohemia	\bar{X}	48.7	41.5	454.6	415.1	378.8	343.2	327.6	300.7	246.9	221.9	524.0	478.0
L = 50.0	SD	2.0	3.6	20.3	23.9	20.6	22.6	17.4	19.6	13.3	16.5	16.4	38.5
	n	21	16	22	17	21	17	22	17	20	15	5	3
Germany	\bar{X}	48.1	40.2	465.2	404.9	384.1	336.8	330.2	291.3	253.9	220.8	509.3	460.5
L = 48.5	SD	3.1	1.7	24.4	18.8	21.9	14.7	17.0	11.3	12.1	12.2	37.4	13.6
	n	22	11	24	13	22	13	23	13	23	13	10	10
Norse	\bar{X}	44.8	42.1	436.8	412.8	344.9	346.5	310.5	301.6	238.9	226.5	496.5	488.4
L = 59.0	SD	4.0	1.0	30.2	21.8	12.6	20.4	20.4	17.7	17.5	9.3	17.4	19.5
	n	12	8	13	8	9	8	12	8	14	8	7	5
England	\bar{X}	48.4	41.1	453.7	414.8	370.3	338.2	329.7	292.9	248.5	218.7	507.6	482.2
L = 51.4	SD	2.2	1.4	25.4	18.9	25.2	15.7	19.1	13.4	14.5	10.8	22.1	22.6
	n	25	25	25	27	25	27	25	27	25	27	15	15
Anglo-Saxon	\bar{X}	na ²	na	458.8	424.0	379.1	351.6	332.6	309.9	251.0	227.1	na	na
L = 52.5	SD			24.4	22.3	23.6	19.4	17.0	15.0	14.3	12.0		
	n			167	66	159	65	165	69	113	53		
France	\bar{X}	46.4	39.6	436.0	400.2	367.6	335.5	311.9	293.1	237.3	216.7	489.3	451.6
L = 44.6	SD	3.5	2.2	19.8	18.5	21.4	19.6	15.5	14.5	14.6	15.6	25.6	21.5
	n	11	9	12	9	13	10	11	10	11	11	10	11
Bosnia	\bar{X}	49.0	42.7	460.3	417.9	385.5	348.5	328.6	299.5	247.3	220.2	501.4	467.0
L = 42.7	SD	2.5	2.3	23.4	21.0	22.3	19.8	17.2	13.9	11.8	13.4	21.3	19.6
	n	43	29	48	31	48	31	48	31	48	28	20	16
N. Africa													
Sudan	\bar{X}	43.5	38.7	455.1	420.4	387.6	357.8	320.2	293.2	251.5	230.2	466.0	428.1
L = 19.7	SD	3.4	2.1	32.5	21.7	30.3	24.2	22.4	14.9	20.0	11.5	36.1	18.2
	n	29	18	30	18	31	18	31	18	31	18	14	10
Nubia	\bar{X}	44.4	38.1	430.1	395.7	370.9	331.9	306.5	277.4	242.5	210.3	463.4	440.0
L = 24.0	SD	3.0	1.7	20.0	15.5	22.9	12.7	14.5	13.2	11.9	7.8	28.0	8.2
	n	13	7	13	7	12	7	13	7	13	7	8	5
Egypt	\bar{X}	44.2	39.2	444.0	414.2	378.0	350.7	312.6	289.5	247.7	227.0	480.7	449.6
L = 30.0	SD	2.8	2.2	19.3	20.1	18.8	17.2	15.4	14.9	13.9	11.8	18.5	15.9
	n	31	36	32	38	30	36	32	37	31	36	8	18
S-S Africa													
W. Africa	\bar{X}	43.4	40.0	452.6	422.0	388.4	359.3	317.4	297.6	258.6	238.2	438.4	437.5
L = 5.0	SD	2.3	3.1	10.4	36.0	15.6	39.7	9.8	18.4	11.5	16.9	34.1	32.4
	n	16	5	16	5	16	4	16	5	16	5	13	3
E. Africa	\bar{X}	43.3	38.8	462.2	424.6	398.8	365.4	330.2	302.2	261.9	237.1	469.3	443.8
L = 2.0	SD	2.7	2.4	28.9	29.3	27.9	24.6	17.0	21.7	13.6	17.9	22.0	31.5
	n	27	19	27	19	27	19	27	19	27	19	11	16
Pygmy	\bar{X}	36.7	35.7	360.7	365.7	308.7	312.7	268.7	270.6	205.3	208.7	420.8	395.4
L = 2.0	SD	2.0	1.9	17.2	19.3	19.6	15.0	17.1	3.5	12.8	14.3	11.6	18.4
	n	7	3	7	3	6	3	7	3	7	3	5	3
San	\bar{X}	38.0	36.3	420.2	387.6	354.8	326.6	291.5	264.9	226.1	201.7	na	na
L = 25.0	SD	1.3	0.9	23.3	19.3	22.7	17.8	19.7	16.1	16.0	15.7		
	n	3	5	12	20	12	21	11	17	11	16		

¹ L = latitude.

² na = data not available.